

# ON THE PROPORTIONS BETWEEN SOME AREAS OF THE FIRST CERVICAL SEGMENT OF THE SPINAL CORD OF PRIMATES

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*Communicated May 27, 1969*

*Abstract.*—It has been generally supposed that the dorsal funiculi occupy a relatively larger part of the highest segments of the spinal cord in man than in any other primate. We have taken planimetric measurements of the total area of the cord, dorsal funiculi, and total gray in the uppermost segments of the spinal cord of a wide variety of primates. Our results indicate that the largest values for the proportions dorsal funiculi/total white matter and dorsal funiculi/ventrolateral funiculi are found in gorilla, chimpanzee, and orang, rather than in man. Moreover, man has, on the average, smaller dorsal funiculi in relation to either the total white or ventrolateral funiculi than any of the three great apes.

The neurologist Brouwer stated in 1915<sup>1</sup> that upon examining the uppermost segments of the cervical spinal cord one could not avoid the conclusion that the tracts carrying what he called the higher functions of sensibility, namely, those of the dorsal funiculi, occupy a relatively larger part of this portion of the cord in man (38.91% of total white matter) than in any other animal. His conclusion was based on measurements taken on cross sections of the highest cervical segment from a series of vertebrates. Using an index which expressed the area of the dorsal funiculi as a percentage of the total area of the white matter, he studied 37 different vertebrate genera, including several primates. Brouwer's primate material was limited to four New World genera, two of the anthropoids, and man. However, curiously, he did not use the two apes (orang and gibbon) in arriving at his conclusions.<sup>1</sup> These conclusions were briefly referred to in his later book,<sup>2</sup> and by other authors.<sup>3</sup> For our investigation we have been fortunate in securing samples of the upper cervical segments of the cord from a variety of primate genera representing all infraorders save the Tarsiiformes. For simplicity we have followed the classification of Fiedler.<sup>4</sup>

*Materials and Methods.*—The material used in this study consists of histological sections obtained from the highest levels (C I) of the cervical spinal cord of 60 normal primates. These specimens came from different collections and had been preserved in various kinds of fixatives (Table 1). For this reason we have had to assume that a possible differential shrinking effect of these fixatives on the white and gray substances or in the different specimens has not been significant to the point of precluding their use in the present investigation.

The blocks of tissue were embedded in celloidin, cut at 30–40  $\mu$  in most cases, and stained by several methods (Modified Loyez, H. & E., Smith-Quigley, Pal-Weigert). The sections were then examined under the light microscope to choose only one to be measured from each animal. The choice was based on the proximity of the section to the spino-medullary junction and on the contrast obtained between gray and white matter by the staining. Tracings of the contours of the whole cord and of the gray substance were done with the help of a Leitz (Prado) microprojector. The machine was placed on a fixed position and the enlarged images focused on a white piece of paper where the outline of

the cord and its components were then drawn with a pencil. The distance between the projector and the paper was kept constant for all of the tracings.

The following measurements were taken on each drawing with a Keuffel and Esser (4236M) compensating polar planimeter: total area of the cord, total area of gray, and total area of the dorsal funiculi. We obtained the value for the total white by subtracting that of the total gray from the total cord, and that for the ventrolateral funiculi by subtracting the dorsal funiculi from the total white. Each measurement was done at least twice by one of the authors and several of them by both authors. The agreement obtained in these independent measurements was extremely close. The divergences ranged between 0 and 7 planimeter units. The values are expressed in planimeter units and not transformed into conventional surface units because our interest is in the proportions existing among the territories measured and not in their absolute values.

The procedure followed with the cord section of the only available mountain gorilla, *Gorilla gorilla beringei*, merits a special comment. The specimen was a poorly preserved one, and half of the best section obtained was very much distorted. For this reason an arbitrary but reasonable midline limit was indicated in the tracing and only the good half used for the measurements. Then, assuming these values to be half of what they would have been in the undisturbed and symmetrical cord, they were doubled and used.

The following decisions had to be made in order to standardize the procedure of measuring. The first relates to the limit between the dorsal funiculus and the ventrolateral white. In a few cases the dorsal horn extended as far as the external surface of the section (*Perodicticus*, Fig. 1), thus separating clearly the two areas of white. More often the boundary between the posteromarginal nucleus and the periphery of the cord could readily be traced; then an arbitrary line was drawn from the end of the posterior horn toward the periphery in such a manner as to correspond to the middle of the fiber bundles from each posterior root (*Gorilla*, Fig. 1). Second, the reticular formation of the lateral funiculus is an area where the separation between white and gray matter is not always easily identifiable. Moreover, in high cervical sections fibers of the decussating pyramidal tract contribute to make this boundary a rather uncertain one. Brouwer<sup>1, 2</sup> included what he was able to identify as the reticular formation with the gray matter, but we found that in tracing the clear-cut cases the part of the section which could be interpreted as the reticular formation was more readily included with the white substance. For this reason, what appeared to us to be the formation was always included with the white in our measurements. In this respect the two procedures, Brouwer's<sup>1, 2</sup> and ours, are not entirely comparable. But the net effect of this difference in procedures is merely one of making the area of the ventrolateral white a bit larger in our measurements.

**Results and Discussion.**—The values of our measurements were used to obtain several indices which express the relative proportions between the measured areas (Table 1). The distribution of these indices is given in Figures 2 and 3, where the corresponding index value is plotted against the brain weight for each animal. All these weights were obtained after fixation of the entire brain. In order to include the specimens of unknown brain weights in the graphs, we used the following procedure. A value equal to the average of the known brain weights of five of our macaques (71.0 gm) was arbitrarily assigned to the two macaques with unknown brain weights. For the five chimpanzees with unknown brain weights we used the average brain weight (274.7 gm) of the six chimpanzees with known values. The average brain weight of all the oranges in our sample (291.2 gm), excluding only the values for the newborn and the fetus, was used to allocate the *Pongo* of unknown brain weight. For the juvenile male gorilla of unknown brain weight we used the average brain weight of all the so-called "young" gorillas in our sample (347.4 gm). Cranial capacities instead of brain weights were employed in the case of the adult male *Hylobates agilis*<sup>5</sup> and the newborn orang.<sup>6</sup>

TABLE 1.

	Age and sex	Brain weight (gm)	Fixative	(DF/TW) <sup>a</sup> × 100	(DF/VLF) <sup>b</sup> × 100
<i>Tupaia</i> sp.			10% Form.	18.2	22.2
<i>Lemur catta</i>		21.6	"	23.0	29.9
<i>Lemur variegatus</i>			"	28.4	39.7
<i>Perodicticus potto</i>			Alcohol	30.6	44.1
<i>Callithrix</i> sp.		34.5	10% Form.	28.1	39.1
<i>Callithrix</i> sp.			Alcohol	22.1	28.3
<i>Lagothrix humboldtii</i>			"	29.5	41.7
<i>Ateles geoffroyi</i>	Late juvenile ♂		10% Form.	26.7	36.5
<i>Ateles</i> sp.		78.5	"	23.0	29.9
<i>Cynopithecus niger</i>	♀		"	31.2	45.3
	Adolescent	71.0 <sup>c</sup>	Form.-Acet.	30.4	43.7
	♀	62.8	10% Form.	30.8	44.5
	♀	63.7	"	28.0	39.0
<i>Macaca mulatta</i>	♀	73.6	"	34.2	52.0
	♂	68.9	"	29.0	40.8
	♂	86.0	"	23.9	31.6
		71.0 <sup>c</sup>	"	30.0	43.8
<i>Hylobates moloch</i>	Adolescent ♀	60.0	Alc.-Form.	36.5	57.1
<i>Hylobates agilis</i>	Adult ♂	103.6 <sup>d</sup>	"	35.1	54.0
<i>Symphalangus syndactylus</i>	Adult ♀	106.0	"	34.7	53.2
		274.7 <sup>e</sup>	10% Form.	40.9	69.0
		274.7 <sup>e</sup>	"	48.8	95.1
		274.7 <sup>e</sup>	"	41.4	70.6
		274.7 <sup>e</sup>	"	37.0	58.7
		274.7	"	37.1	59.1
<i>Pan</i> sp.		264.0	"	45.8	84.5
		284.0	"	40.4	67.8
		236.0	"	37.4	59.7
		272.0	"	36.3	57.0
		282.0	"	39.1	64.3
		310.0	"	40.2	67.2

Form., formaldehyde; Alc., alcohol; Acet., acetic acid.  
<sup>a</sup> Percentage of dorsal funiculi to total white matter. <sup>b</sup> Percentage of dorsal funiculi to ventrolateral funiculi. <sup>c</sup> Brain weight =  $\bar{x}$  all macaques in our sample. <sup>d</sup> Cranial capacity (ref. 5). <sup>e</sup> Brain

We have assumed that these values will not differ too widely from the corresponding brain weights. The information about age and sex of the specimens at our disposal was too fragmentary to allow its use in any other way than that noted above.

It can be observed that, contrary to what Brouwer asserted,<sup>1, 2</sup> adult man (29.8–38.4, Table 1, Fig. 2) is surpassed in the proportion dorsal funiculi/total white by *Gorilla* (range for all gorillas in our sample 36.7–52.3, Table 1, Fig. 2), *Pan* (range for all chimpanzees in our sample 36.3–48.8, Table 1, Fig. 2), and *Pongo* (range for all orangs in our sample except the fetus 33.3–48.5, Table 1, Fig. 2). In the proportion dorsal funiculi/ventrolateral funiculi, adult man (42.3–62.2, Table 1, Fig. 3) is again surpassed by the available gorillas (58.0–109.6, Table 1, Fig. 3), chimpanzees (57.0–95.1, Table 1, Fig. 3), and orangs (49.9–94.1, Table 1, Fig. 3), except the fetus. In order to estimate the significance of the difference between the index values for man and each of the three great apes, we decided to treat all the available members of each pongid genus as forming a homogeneous sample for our purposes. Only the fetal orang was excluded from our calculations. More reliable results would be obtained by using larger samples

TABLE 1. (continued)

	Age and sex	Brain weight (gm)	Fixative	(DF/TW) <sup>a</sup> × 100	(DF/VLF) <sup>b</sup> × 100
<i>Pongo pygmaeus</i>	Adult	291.2 <sup>f</sup>	Alcohol	42.4	73.6
	Adult			37.3	59.6
	Adult			37.6	60.3
	Fetus ♂	20.0	Alc.-Form.	22.6	29.0
	Newborn ♀	129.1 <sup>g</sup>	10% Form.	35.7	55.6
	Adolescent ♀	267.0	Alc.-Form.	33.3	49.9
	" ♀	274.0	"	48.5	94.1
	" ♂	298.0	"	41.0	69.2
	Young ♂	298.0	"	38.2	61.9
	Adult ♀	279.0	"	34.2	51.9
	Adult ♀	287.5	"	33.3	50.0
	Adult ♂	335.0	"	44.2	79.2
	♀	350.0	"	48.8	95.4
	Infant ♀		"	40.4	67.6
<i>Gorilla gorilla gorilla</i>	Young	247.0	"	44.1	79.9
	Young ♀	327.0	"	45.8	84.5
	Young ♀	319.0	"	42.7	74.5
	Juvenile ♂	347.4 <sup>h</sup>	"	41.0	69.4
	Adult ♀	407.0	"	36.7	58.0
	Adult ♂	510.0	10% Form.	42.1	72.6
<i>Gorilla gorilla beringei</i>	Young ♂	496.6	Alc.-Form.	52.3	109.6
<i>Homo sapiens</i>	Adult			30.5	43.9
	Adult			29.8	42.3
	"			35.8	55.7
	"			33.2	49.6
	"			38.4	62.2
	"			35.2	54.3
	"			35.3	54.6
	"			37.5	59.9

weight =  $\bar{x}$  all chimpanzees in our sample. <sup>f</sup> Brain weight =  $\bar{x}$  all orangs in our sample less fetus and newborn. <sup>g</sup> Cranial capacity (ref. 6). <sup>h</sup> Brain weight =  $\bar{x}$  all "young" gorillas in our sample.

which were also more homogeneous in age and sex for each genus. Unfortunately, we were unable to secure any better information in this respect than that presented in Table 1. It should be pointed out that the determination of age level for the various specimens was not done by the authors of this work; therefore, it is possible that different criteria might have been originally employed. In addition, no definite discernible trend characterizes the distribution of either index when arranged according to our data regarding the age and sex of the specimens. Our results indicate that the difference between the average values of the indices expressing the dorsal funiculi as a proportion of the total white matter for the 8 men and the 11 chimpanzees in our sample is statistically significant ( $t = 3.578$ ;  $p < 0.01$ ); it is also significant for the same men and the 11 orangs ( $t = 2.152$ ;  $p \simeq 0.03$ ), and for the men and the 9 gorillas ( $t = 4.774$ ;  $p < 0.01$ ). A similar analysis for the dorsal funiculi/ventrolateral funiculi proportion shows that the differences between the 8 men in our sample and the representatives of each pongid genus are also significant: man-chimpanzee ( $t = 3.33$ ;  $p < 0.01$ ), man-orang ( $t = 2.118$ ;  $p \simeq 0.03$ ), and man-gorilla ( $t = 4.358$ ;  $p < 0.01$ ).

It is evident that values larger than those expressing the proportions dorsal

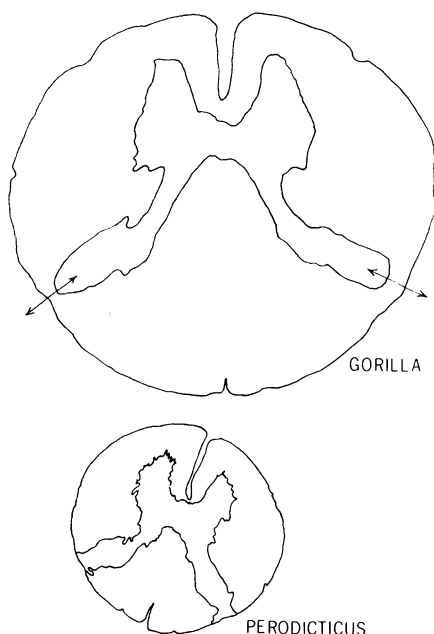


FIG. 1.

funiculi/total white and dorsal funiculi/ventrolateral funiculi for man can be found in any of the three pongids, and, what is more important, that man appears to have, on the average, smaller values for each of these two proportions than chimpanzee, orang, and gorilla. At the present time and on the basis of our results, we can only speculate on the significance of these findings. Our data (Table 1, Figs. 2 and 3) support the view<sup>1-3</sup> that there is a phylogenetic increase in the relative size of the dorsal funiculi in the highest segments of the cord of primates; this is evident when one begins with the tree shrew, *Tupaia*, passes up through the lemurs and monkeys, and so on to the apes and man (Figs. 2, 3; Table 1). Such a progressive enlargement is probably related to changes in body size and is in all likelihood the result of an increase in the

number of fibers; but this is not an established fact. If this does occur, it would be of interest to find out what kind of changes, if any, occur in the fiber composition of the functional components of the dorsal funiculi in the highest segments of the various primate cords, particularly in relation to the different locomotive habits of the animals.

That the dorsal funiculi are related to "a sense which enables the animal to appreciate postures of the limbs and continuity of movement" was shown by Ferraro and Barrera.<sup>7</sup> Lesion of the dorsal columns above the levels supplying both extremities produced a more intense loss of this sense in the arms than in the legs.<sup>7</sup> More recent experiments<sup>8</sup> have largely confirmed these results. Gardner<sup>9</sup> has reviewed and discussed the evidence which assigns to the dorsal columns the pathways for impulses arising from movements of the joints and from mechanical deformation of the deep tissues and skin. He also discussed the evidence for other pathways that can be followed by these same impulses to reach higher centers. These pathways, however, arise from connections established in the gray matter by collaterals of the primary afferent fibers which run in the dorsal funiculus.<sup>9</sup> With these facts in mind, the following tentative explanation can be given for the dorsal funiculi/total white and dorsal funiculi/ventrolateral funiculi proportions which we have observed in the three great apes and man. It is conceivable that the larger values obtained for the pongids might be due to the presence in the highest cervical segments of their dorsal white matter of a relatively larger number, in contrast to man, of sensory fibers subserving the sense of position and movement from the upper limb.<sup>10</sup>

Admittedly, the adult forms of both African great apes are basically terrestrial in their locomotive behavior, but the feeding and nesting activities of the chim-

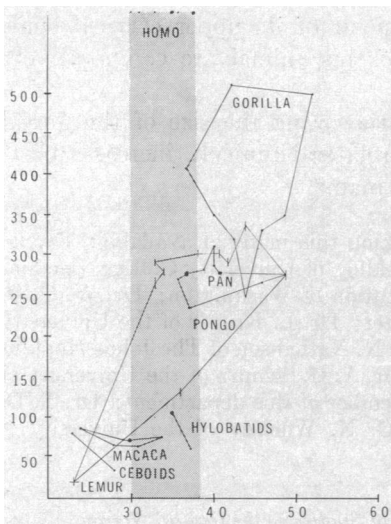


FIG. 2.—Perpendicular scale shows brain weights in grams, and the horizontal scale gives the dorsal funiculi/total white percentage. This graph includes only those specimens from Table 1 for which brain weight was known or to which a brain weight value could be assigned as explained in the text. Where two specimens coincide in the same point in the graph, this is indicated by a thicker mark (●).

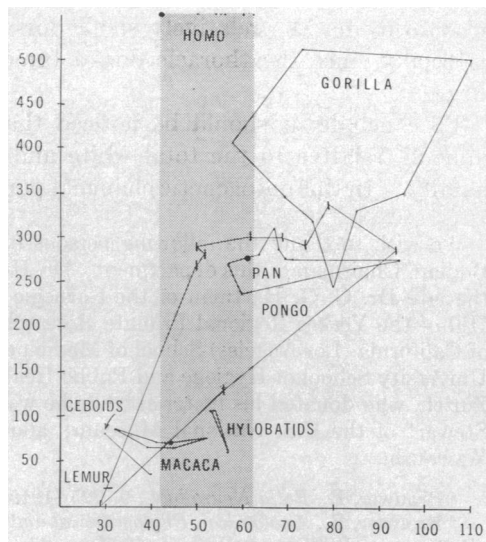


FIG. 3.—Perpendicular scale shows brain weights in grams, and the horizontal scale gives the dorsal funiculi/ventrolateral funiculi percentage. This graph includes only those specimens from Table 1 for which brain weight was known or to which a brain weight value could be assigned as explained in the text. Where two specimens coincide in the same point in the graph, this is indicated by a thicker mark (●).

panzee are more arboreal than those of the gorilla.<sup>11-16</sup> The adult orang, on the other hand, is almost entirely arboreal in its locomotive as well as in its feeding and nesting behavior.<sup>17, 18</sup> Although all the great apes retain the musculoskeletal pattern and proportions associated with the capacity to brachiate,<sup>19-24</sup> recent field observations show that only the orang<sup>17, 18</sup> and the chimpanzee<sup>12, 14, 25, 26</sup> engage in occasional brachiation at all stages of postnatal life. It is possible, therefore, that the postulated presence in the dorsal funiculi of the three great apes of a larger number of sensory fibers subserving the sense of position and movement in the upper limb is the result of an early evolutionary adaptation to a more acrobatic type of arboreal locomotion than that which they—particularly the chimpanzee and, above all, the gorilla—practice today. The fact that the gibbon, the brachiator *par excellence*, has not such relatively large dorsal funiculi, thus herein more closely resembling man (Table 1, Figs. 2 and 3), will appear to contradict our interpretation. It is quite possible, however, that the low values of the hylobatids may well be related to the smaller size of these apes.

The small values observed in a presumably mature spider monkey (Table 1, Figs. 2 and 3) might be related to the peculiarities of this genus. The locomotive habits of *Ateles* involve extensive use of the tail and all four limbs, and the animal is known to brachiate very effectively.<sup>20, 27, 28</sup> All these data would lead one to expect proportionately larger dorsal columns in the cervical region. However, the absence of a thumb in the spider monkey might well be an important factor

accounting for the relatively small dorsal funiculi of its upper cervical cord, especially since the thoracic dorsal funiculi of this animal are comparatively large.<sup>29</sup>

To conclude, it should be noticed that in the orang the size of the dorsal funiculi, relative to the total white and ventrolateral funiculi, increases post-natally. In this ontogenetic change it parallels man.<sup>30</sup>

We wish to thank the following persons for making this material available: Dr. D. Bodian, Chairman of this department; Dr. Una Fielding of University College, London; the late Dr. C. G. Hartman of the Carnegie Institution of Washington; Dr. W. C. O. Hill of the Yerkes Regional Primate Research Center; Dr. L. Kruger of the University of California (Los Angeles) School of Medicine; Dr. N. Nathanson of The Johns Hopkins University School of Hygiene and Public Health; Dr. A. H. Schultz of the University of Zürich, who donated his material while he was a member of this department; Dr. T. D. Stewart of the U.S. National Museum; and Dr. C. N. Woolsey of the University of Wisconsin.

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